Biological Synopsis of the Asian Shore Crab, *Hemigrapsus sanguineus*

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by

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ABSTRACT

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The Asian shore crab is native to northern Asia, from Sakhalin Island (Russia) to Taiwan, where it experiences water temperatures of <0°C in winter to 28°C in summer. It has established populations in the Atlantic from North Carolina to central Maine and from the English Channel to Germany, and has been reported from the Black Sea and northern Adriatic Sea. The species is not yet found in eastern Canada, but its potential distribution may include the Bay of Fundy and southern Nova Scotia. Natural dispersal is by planktonic larvae and benthic adults and juveniles. Shipping vectors have been implicated in anthropogenic dispersal.

Low-energy, intertidal, boulder/cobble beaches are the characteristic native habitat. In North America, the crabs also utilize sand/pebble beaches, mussel beds, eelgrass beds, salt marshes, and artificial structures including aquaculture gear. The diet of the Asian shore crab includes algae, marine grasses, and invertebrates. Competition has been reported with native crabs that inhabit intertidal and subtidal habitats.

RÉSUMÉ

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Le crabe sanguin est indigène du nord de l'Asie, de l'île de Sakhaline (Russie) à Taïwan, où il tolère des températures d'eau inférieures à 0°C en hiver et atteignant jusqu'à 28°C en été. Il a établi des populations dans l'Atlantique de la Caroline du Nord jusqu'au centre du Maine et de la Manche jusqu'en Allemagne. Sa présence a été signalée dans la mer Noire et dans la partie nord de la mer Adriatique. Le crabe sanguin n'a toujours pas été repéré dans l'est du Canada, mais sa répartition potentielle pourrait inclure la baie de Fundy et le sud de la Nouvelle-Écosse. Sa dispersion naturelle se produit par le biais des larves planctoniques et des adultes et des juvéniles benthiques. Les vecteurs liés à la navigation jouent un rôle dans la dispersion anthropique.

Les plages intertidales à faible énergie, composées de grosses pierres et de galets constituent l'habitat indigène caractéristique de l'espèce. En Amérique du Nord, les crabes habitent également les plages de sable et de cailloux, les moulières, les herbiers de zostère, les marais salés ainsi que les structures artificielles, notamment les installations aquacoles. Le crabe sanguin se nourrit des algues, des herbes marines et des invertébrés. Une compétition avec les crabes indigènes qui habitent les zones intertidales et infratidales a été rapportée.

1 INTRODUCTION

1.1 NAME AND CLASSIFICATION

Kingdom: Animalia
Phylum: Arthropoda
Subphylum: Crustacea
Class: Malacostraca
Subclass: Eumalacostraca
Superorder: Eucarida
Order: Decapoda
Suborder: Pleocyemata
Infraorder: Brachyura
Superfamily: Grapsoidea
Family: Varunidae
Genus and species: *Hemigrapsus sanguineus* (de Haan, 1853)
Common name: Asian shore crab, Japanese shore crab

(source: Integrated Taxonomic Information System (ITIS 2011))

1.2 DESCRIPTION

The carapace is square, with three teeth on each side (Figure 1). Colour is mottled or dotted with reddish brown, greenish, or dark purple areas. The dorsal side of the chelipeds is speckled with small dark purple-red dots. Other periopods display a distinctive pattern of alternating light and dark transverse stripes. There are no antero-ventral black dots on the body or chelae, differentiating *H. sanguineus* from some other species in the genus. Males have a small fleshy swelling (vesicle) at the base of the dactylus of the cheliped. Female and juvenile crabs have no fleshy vesicle. Obert et al. (2007) indicated that this vesicle collapses within 1–2 hr when the crab is preserved in ethanol. Maximum size reported is 43.9 mm carapace width (CW) (McDermott 1998).

Breton et al. (2002) and D'Udekem d'Acoz (2006) provided descriptions and figures to differentiate *Hemigrapsus sanguineus* from its congener, the pencil crab or brush-clawed shore crab (*H. takanoi*), which has also established invasive populations in Europe.

The first zoeal stages of six species of *Hemigrapsus* from the northern Pacific Ocean, including Asian shore crab, were described with an identification key by Lee and Ko (2008). The lack of a spinulate tip on the antennal exopod differentiates the two Pacific North American species from the four Asian species included in the key. Zoeal stage I of Asian shore crab differs from the other three Asian species of *Hemigrapsus* on the basis of having lateral processes on abdominal pleomeres 2 and 3, and the presence of 1 large and 2 smaller medial spines on the antennal exopod.

(source: http://upload.wikimedia.org/wikipedia/commons/3/38/Hemigrapsus_sanguineus.jpg, accessed 12 January, 2012)

Figure 1. Adult male *Hemigrapsus sanguineus*

A key to the identification of the first zoeal stage and the megalopae of the known Varuninae, including eight species of *Hemigrapsus*, was presented by Kim and Hwang (1995).

Characters of the first zoeal stage were contrasted to other members of the Grapsidae by Cuesta and Schubart (1997).

In contrast to the above authors, Kornienko et al. (2008) stated that zoeal stages I and II of *Hemigrapsus sanguineus*, *H. penicillatus*, and *H. longitarsis* are indistinguishable. They presented a key for zoeae III through V and the megalopa stage.

No *Hemigrapsus* species are native to the east coast of North America. In British Columbia, there are two native *Hemigrapsus*: the purple shore crab *H. nudus* (Dana, 1851) and the green shore crab *H. oregonensis* (Dana, 1851) (Hart 1984; Baldwin 2010).

1.3 GENETICS

Upon examination of 525 DNA nucleotides corresponding to the 16S mtDNA gene, an Asian shore crab detected in Croatian waters was found to be identical to a specimen from Massachusetts and matched 474 nucleotides in a specimen from Japan (Schubart 2003). In contrast, a specimen obtained from Taiwan differed in two positions (two transitions) from the Croatian, American, and Japanese specimens. Steinberg (2008) similarly determined that Japan or Northern China were the most likely originating

populations for the invasion of the eastern USA. Crabs from Hong Kong had different gene sequences.

Polymorphisms of 17 enzymes and genetic variations of Asian shore crab from Miyagi, Japan were examined using starch gel electrophoresis (Chow and Fujio 1987). COI sequences were described by Darling and Tepolt (2008).

2 DISTRIBUTION

2.1 NATIVE DISTRIBUTION

Sakai and others noted that the Asian shore crab is native to Sakhalin Island (Russia), Korea, Japan, North China, Hong Kong, and Taiwan (Gerard et al. 1999; D'Udekem d'Acoz 2006). The latitudinal native range in the northwestern Pacific is approximately 22° N to 50° N (McDermott 1998) (Figure 2).

2.2 NON-NATIVE DISTRIBUTION

Asian shore crab has established reproducing populations on the northwestern and northeastern shores of the Atlantic Ocean, and inoculations (but no evidence of establishment) have been reported from the Black Sea and northern Adriatic Sea (Figure 2; Table 1 and Table 2).

2.2.1 North America

In the USA, the crab is currently established from Oregon Inlet, North Carolina (NC), to the Schoodic Peninsula, Maine (ME) (Table 1). It was first reported from the coast of New Jersey (NJ) in 1988 with the discovery of a single female specimen thought to be at least three years of age (Williams and McDermott 1990).

2.2.2 Europe

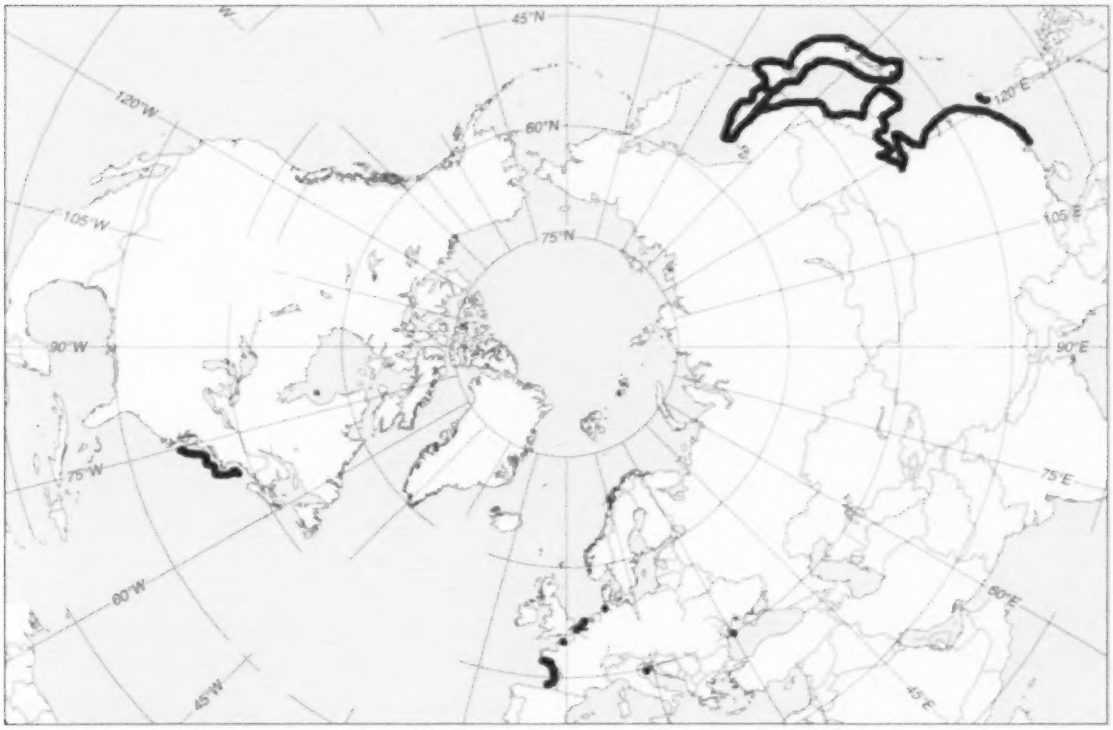
In Europe, the distribution of established populations of the Asian shore crab extends from the west coast of the Cotentin Peninsula in the English Channel to the Lower Saxony state of Schleswig-Holstein, Germany (Table 2).

The first Asian shore crabs in Europe were most likely those recorded near Le Havre, France in 1999. Because the discovery was of an adult breeding population, they were thought to have settled there in, or before, 1998 (Breton et al. 2002). A second discovery at Oosterschelde, the Netherlands, in 1999, yielded only two male crabs, despite an intensive investigation of the site (Breton et al. 2002).

Asian shore crab has been observed in the Mediterranean only once, in August 2001, in the northern Adriatic (Schubart 2003). A single adult male specimen was collected from under a large boulder on a rocky platform at sea level in Uvala Slanik on the northwestern coast of Istra, between Umag and Novigrad in Croatia.

One adult male (20.7 mm CW) was collected inside Tomis Marina, Romania, near Constanta Sud-Agigea, in the Black Sea (Micu et al. 2010). The specimen was found

under a rock just above the waterline. The ability of Asian shore crab to successfully establish a reproducing population in the Black Sea was questioned by Micu et al. (2010), as the surface water salinity in the Romanian sector varies between 13 and 17 ‰, and the maximum surface water salinity of the Black Sea, as a whole, was only 18.5 ‰.



(Figure by G. Klassen)

Figure 2. Worldwide distribution of Asian shore crab

(Indicated by solid black line along coastline of Asia (native populations), eastern North America (established introduced population) and Europe (established introduced population). Points in the northern Adriatic and Black seas indicate recent inoculations for which establishment has not been confirmed.)

Table 1. Partial list of introduced populations of Asian shore crab in the United States of America, ordered from north to south, showing year of first observation

State*	Location	Latitude (°N)	Longitude (°W)	Year	Reference
ME	Schoodic Peninsula (northeast limit of Acadia National Park)	44.362	68.078	2005	Delaney et al. 2008
ME	Lowell Cove Orr's Island	43.759	69.976	2004	Stephenson et al. 2009
ME	Cape Elizabeth	43.599	70.199	2004	Stephenson et al. 2009
ME	Biddeford Pool	43.440	70.343	2004	Stephenson et al. 2009
ME	Kittery	43.091	70.660	2004	Stephenson et al. 2009
MA	Green Harbor	42.078	70.652	1994	McDermott 1998

State*	Location	Latitude (°N)	Longitude (°W)	Year	Reference
MA	East end of Cape Cod Canal	41.775	70.465	1994	McDermott 1998
MA	Buzzards Bay	41.730	70.627	1994	McDermott 1998
MA	Woods Hole	41.523	70.673	1992	McDermott 1998
CT	Milford	41.207	73.053	1993	McDermott 1998
NY	Rye	40.968	73.630	1994	Kraemer et al. 2007
NY	Pelham Bay (Bronx)	40.857	73.810	1994	McDermott 1998
NJ	Townsends Inlet Bridge (Cape May County)	38.935	74.911	1988	Williams and McDermott 1990
VA	Cape Charles	37.266	76.051	1993	McDermott 1998
NC	Oregon Inlet (Pamlico Sound)	35.770	75.535	1995	McDermott 1998

*CT (Connecticut); MA (Massachusetts); ME (Maine); NC (North Carolina); NJ (New Jersey); NY (New York); VA (Virginia)

Table 2. Published records of Asian shore crab in Europe, including year of first observation

Country	Location	Latitude (°N)	Longitude (°E or W)	Year	Reference
Germany	Schleswig-Holstein	54.516	9.569 E	2006	Obert et al. 2007
Germany	Lower Saxony (Island of Noderney)	53.709	7.148 E	2007	Obert et al. 2007
The Netherlands	Nieuwpoort-Bad	51.154	2.706 E	2006	Nuyttens et al. 2006
The Netherlands	Western Scheldt	51.855	4.047 E	1999 2004	Faasse 2004 and Nijland and Faasse 2005 (both cited in D'Udekem d'Acoz 2006)
The Netherlands	Hoek van Holland	51.976	4.132 E	2003	Campbell and Nijland 2004
The Netherlands	Schelphoek, Oosterschelde (Eastern Scheldt)	51.691	3.818 E	1999	Breton et al. 2002; D'Udekem d'Acoz and Faasse 2002
Belgium	Albertstrand	51.347	3.275 E	2006	D'Udekem d'Acoz 2006
Belgium	Duinbergen	51.346	3.260 E	2006	D'Udekem d'Acoz 2006
Belgium	Nieuwpoort	51.352	3.295 E	2006	Nuyttens et al. 2006
France	Le Havre	49.486	0.106 E	1999	Breton et al. 2002
France	La Hougue, Cotentin Peninsula	49.575	1.272 W	2008	Dauvin 2009a,b
France	Saint-Vaast, Cotentin Peninsula	49.593	1.263 W	2008	Dauvin 2009a,b
France	Gatteville-Phare, Cotentin Peninsula	49.696	1.266 W	2008	Dauvin 2009a,b
France	Salines, Cotentin Peninsula	49.658	1.646 W	2008	Dauvin 2009a,b
France	Querqueville, Cotentin Peninsula	49.669	1.680 W	2008	Dauvin 2009a,b
France	Goury, Cotentin Peninsula	49.715	1.946 W	2008	Dauvin 2009a,b
France	Gonneville, Cotentin Peninsula	49.083	1.612 W	2008	Dauvin 2009a,b

Country	Location	Latitude (°N)	Longitude (°E or W)	Year	Reference
France	Blainville sur mer, Cotentin Peninsula	49.059	1.613 W	2008	Dauvin 2009a,b
France	Agon-Coutainville, Cotentin Peninsula	49.025	1.600 W	2008	Dauvin 2009a,b
France	Granville, Cotentin Peninsula	48.833	1.608 W	2008	Dauvin 2009a,b
France	Berck-Authie, Opal coast	50.393	1.558 E	2008	Dauvin et al. 2009
France	Le Portel, Opal coast	50.708	1.560 E	2008	Dauvin et al. 2009
France	Boulogne Harbour, Opal coast	50.725	1.567 E	2008	Dauvin et al. 2009
France	Wimereux, Opal coast	50.751	1.595 E	2008	Dauvin et al. 2009
France	Ambleteuse, Opal coast	50.803	1.599 E	2008	Dauvin et al. 2009
France	Audresselles, Opal coast	50.831	1.589 E	2008	Dauvin et al. 2009
France	Gris Nez Cape, Opal coast	50.872	1.588 E	2008	Dauvin et al. 2009
France	Blanc Nez Cape, Opal coast	50.928	1.709 E	2008	Dauvin et al. 2009
France	Calais Harbour, Opal coast	50.968	1.842 E	2008	Dauvin et al. 2009
France	Dunkirk Harbour, Opal coast	51.051	2.368 E	2005	Dauvin et al. 2009
Croatia	Between Umag and Novigrad on the Peninsula of Istra, Northern Adriatic Sea	45.391	13.482 E	2001	Schubart 2003
Romania	Constanta (Black Sea)	44.170	28.638 E	2010	Micu et al. 2010

2.3 DISTRIBUTION IN CANADA

As of December, 2011, *H. sanguineus* has not been reported in Canadian waters.

2.4 MODES OF INVASION

Natural dispersal of Asian shore crab occurs by means of the planktonic larvae, carried on ocean currents, or as benthic adults.

Shipping vectors are typically implicated in dispersal outside the native range. McDermott (1998) suggested that Asian shore crab was probably introduced to the USA via ballast water at one or more major shipping centres south of Cape Cod (i.e., the New York Bight, Delaware Bay, Chesapeake Bay), perhaps in the early 1980s. Similarly, Breton et al. (2002) suggested that ballast water was the likely vector to Europe, since the initial report at Le Havre involved the discovery of several dozen crabs, perhaps indicating the settlement of a group of transported larvae. Ballast water was not considered by Micu et al. (2010) to be the shipping vector responsible for transport to the Black Sea. Only one specimen was discovered there and it was found inside a marina, which led Micu et al. (2010) to conclude that yachts were the vector of

introduction and that a juvenile or adult specimen, rather than planktonic larvae, had been transported.

3 BIOLOGY AND NATURAL HISTORY

3.1 LIFE HISTORY

The life history of Asian shore crab consists of planktonic larval, and benthic juvenile and adult forms. Crabs with a carapace width (CW) <12 mm are considered juvenile (McDermott 1998; Gerard et al. 1999).

In Japan, ovigerous females incubated their embryos from April to July (Saigusa and Kawagoye 1997). The highest proportion of ovigerous females in the population was found in May (Saigusa and Kawagoye 1997). Females may live for at least three years and the largest females were capable of producing more than five broods/year, with as many as 56,000 eggs/brood (Fukui 1988). McDermott (1991), on the basis of preliminary data, suggested that crabs in New Jersey might be producing larger broods at a given body size than those in Japan.

In New Jersey, ovigerous females occurred from late April through September (McDermott 1998). At Greenwich Point, CT, the percentage of females that were ovigerous increased over the summer to a peak of 62% in early August (Ahl and Moss 1999).

In New Jersey, a CW of approximately 12 mm was the minimum size at which females were observed to become ovigerous and at least two broods of embryos were produced in a season (McDermott 1998). Recruitment of new crabs began as early as June, and continued throughout the summer into the fall and winter. The peak of crabs <10 mm observed March–April represented the previous year's recruitment, and was followed in June by a new cohort of crabs <6 mm. By September–October, this cohort was represented by a second annual peak of crabs <10 mm (McDermott 1998). Similarly, population maxima at Rye, NY, occurred in the intertidal zone in September (Kraemer et al. 2007).

Ovigerous females (12 to 27 mm CW) at Crane Neck Point, NY, were most common in summer. Very small crabs became abundant in fall, and immature crabs of indeterminate gender were abundant in winter (Gerard et al. 1999).

Mating was initiated by the male, and both males and females had calcified exoskeletons at the time of copulation (Anderson and Epifanio 2010a). Mating differed from other species in the genus in terms of positioning during mating, which was vertical with ventral surfaces facing, probably facilitating some degree of mobility in the pair. Females were receptive to copulation within a few days of larval release, and were capable of storing sperm and producing at least two broods from a single copulation. Mean incubation time of newly extruded eggs was around 16–17 d at 25°C (although Epifanio et al. (1998) had determined incubation time as 14 d under the same conditions), and females often produced a second brood within a few days of larval

release. An individual Asian shore crab could produce two broods within 40 days. No females were observed to produce a third brood from the stored sperm.

In the field, larval release always occurred near the time of nocturnal high tide (Park et al. 2005). This pattern of release minimized the impact of visual predators on newly hatched zoeae and took advantage of water circulation to transport zoeae away from intertidal habitats where conditions may not be favourable for larval development.

In the laboratory, larval release coincided with the times of high tide in the field, primarily at higher high tides but sometimes at lower high tides (Saigusa and Kawagoye 1997). When the nocturnal high tide occurred near the time of lights-on in the lab, females shifted the timing of larval release to the opposite high tide. As well, larval release occurred at higher high tide around the full and new moons, but on lower high tides at the half moon. Palmer (1997) further noted that larval release in this species involves an individual shedding all its larvae in approximately a 6-hr interval. At the population level, this release would occur 25 hr later each day and would be synchronized with the time of high tide.

3.2 LARVAL DEVELOPMENT

There are five zoeal stages and a megalopa stage in larval development.

In the Middle Atlantic Bight (Delaware), eggs hatched 14–17 days after extrusion (25°C, 30 ‰) (Anderson and Epifanio 2010a; Epifanio et al. 1998). Females had the potential to produce several broods each year during the spawning season of approximately 4 months (Epifanio et al. 1998). Newly extruded egg masses were bright orange, gradually changed to dark brown, and then changed to brownish green as development proceeded. (An index has been developed to relate the colour of an egg mass to the developmental state of embryos within the eggs.) Newly hatched zoeal larvae had a mean dry weight of 11.4 μg (Epifanio et al. 1998).

An entire brood was hatched over a period of 3–6 h at 24°C in the laboratory. When hatching was imminent, the seawater foamed in the beaker, possibly because of mucus released by the female (Saigusa and Kawagoye 1997).

The duration of larval development was dependent on environmental conditions. Zoeal larvae were tolerant of many temperature-salinity combinations (Table 3), and mean duration of zoeal development ranged from approximately 16 d at 25°C to 54 d at 15°C (Epifanio et al. 1998). At 25°C, zoeae were capable of development to the megalopa stage at salinities as low as 15 ‰. At 15°C, the zoeae required salinities above 20 ‰ for development. No larvae survived beyond zoeal stage II at a salinity of 10 ‰, regardless of temperature. Survival to the megalopa stage reached 60% under favourable conditions. Growth was greatest at 25°C and at salinities of 20 to 30 ‰. Larvae held under these conditions attained approximately three times the weight of larvae held at 15°C. The maximum dry weight of a zoea before moulting to the megalopa stage was 210 μg.

Table 3. Mean percentage survival of *Hemigrapsus sanguineus* (and mean duration of development, in days) from hatching to the megalopa stage at different combinations of temperature and salinity.
(Data from Epifanio et al. 1998)

Salinity	Temperature		
(‰)	15 °C	20 °C	25 °C
10	0	0	0
15	0	0	8.3% (21.8 d)
20	0	23.3% (22.8 d)	60.0% (16.4 d)
25	3.3% (54.5 d)	60.0% (21.5 d)	50.0% (15.9 d)
30	5.0% (53.0 d)	60.0% (20.8 d)	46.7% (15.6 d)

The megalopa stage appeared to have more stringent temperature-salinity requirements than the zoea, which may restrict settlement of Asian shore crab to the coastal zone and high-salinity regions of estuaries (Epifanio et al. 1998). No megalopae survived to crab stage I at 15°C or at salinities below 25 ‰. At 25°C and 30 ‰, megalopae moulted to the first juvenile stage in approximately 25 d post hatching, with mean survival of 17%. The dry weight of megalopae shortly before metamorphosis reached 475 μg.

After moulting to the postlarval (megalopal) stage, Asian shore crab megalopae gained competency (the ability to undergo metamorphosis) after 3 days in conditions of 25°C, 30 ‰, and 14 h light:10 h dark cycle (Kopin et al. 2001). Mean time to metamorphosis varied with environmental cues and was shortest for conspecific exudate (6.9 days) relative to exudate from other species (~9–10 days), and for intertidal pebble substrate (6.55 days) relative to muddy substrate with or without vegetation (~11 days) (Kopin et al. 2001). Reducing the time to metamorphosis was suggested to enhance rates of recruitment and survival (Anderson and Epifanio 2009). Biofilms composed of extracellular polymeric substances produced by diatoms, bacteria, protozoa, and fungi were found to reduce time to metamorphosis. Previous studies, such as those of Kopin et al. (2001), determined that metamorphosis is accelerated by the presence of biofilm from rocky intertidal habitat. Megalopae exposed to 8-day biofilm underwent metamorphosis in approximately 6.5 days, as compared to those exposed to less mature biofilm, or to control treatments (8–9 days to metamorphosis). Megalopae exposed to unmodified biofilmed rock or to abiotic rock had shorter time to metamorphosis than those exposed to a biofilm-exudate solution or artificial seawater control. Exposing biofilmed rock to -20°C for 12 h and then warming to 25°C did not affect the time to metamorphosis, but the settlement cue was de-activated by heating the rock to 100°C for 10 min. Accelerated metamorphosis associated with biofilm from rocky intertidal habitat occurred only after the concentration of microorganisms exceeded a certain threshold; in this study, the threshold was achieved after 8 days and the cell concentration had reached ~4 x 10^7/cm^2.

3.3 AGE AND POST-SETTLEMENT GROWTH

Newly metamorphosed crabs reached the fifth juvenile instar in 35 days or less at 25°C and 30 ‰ (Epifanio et al. 1998). Growth in carapace width was linear at a rate of 0.06 mm/d. Dry-weight growth of zoeal larvae and early stage juveniles was exponential at

respective rates of 23% and 8% of body weight per day. After 35 d growth, juveniles had reached a mean dry weight of more than 8 mg. Assuming continued linear growth in carapace width, female crabs would reach maturity in approximately 7.5 months. Because growth probably ceased during the coldest winter months, it is more likely that crabs would reach maturity about 1 year after metamorphosis.

In Japan, newly settled juveniles had a mean carapace width (CW) of ~2 mm and reached 20 mm in about 2 years (Fukui 1988). They became reproductively mature at this age. The maximum sizes reported for the species in Japan were 42.4 mm and 39.0 mm for males and females, respectively, corresponding to a maximum lifespan of around eight years.

In New Jersey, crabs ranged in carapace width from 2.3 to 43.9 mm CW (McDermott 1998). The largest female collected was the first crab detected in the USA, an ovigerous specimen (35.8 mm CW).

McDermott (1998) calculated the relationship of carapace length (CL, in mm) to carapace width (CW, in mm), and log wet weight (WW, in g) to log carapace width for male and female Asian shore crabs collected in New Jersey from 1988 to 1996 as follows:

Male:

CL = 0.19332 + 0.86824 CW	R^2=0.999, n=605
Log WW =-3.5067 + 3.1320 log CW	R^2=0.996, n=224

Female:

CL = 0.22805 + 0.84948 CW	R^2=0.998, n=481
Log WW = -3.4266 + 3.0150 log CW	R^2=0.996, n=162

Males were heavier than females at equivalent CW as the chelipeds were larger. The smallest male and female crabs (<3 mm CW) weighed <0.010 g (WW). The largest male (43.9 mm CW) and female (31.1 mm CW) weighed 39.0 g and 10.3 g respectively. The 35.8 mm CW female was not weighed, but based on the equation would have weighed ~18 g (McDermott 1998).

The largest crabs found at Greenwich Point, CT in 1997 were 36 mm CW (male) and 25 mm CW (female) (Ahl and Moss 1999). The smallest ovigerous female they collected was 12 mm CW (Ahl and Moss 1999).

In France, Dauvin (2009b) indicated three size modes in the population were probably age-related: crabs of 6–8 mm (and up to 10 mm) were young of the year; 18–20 mm were age 1; 30–32 mm were >2 years. The smallest ovigerous female was 13 mm and the largest was 31 mm. The largest male was 34 mm.

McDermott (1998) suggested that the largest male (43.9 mm CW) collected in his study had probably reached its terminal moult (terminal anecdysis). In contrast, however,

Hartnoll (1983) stated that *Hemigrapsus sanguineus* had indeterminate growth and no terminal anecdysis.

3.4 HABITAT

In its native range, the rocky intertidal zone has been generally considered to be the characteristic habitat of the Asian shore crab (Fukui 1988) (see exceptions noted below), whereas in North America, the crab became widely distributed throughout the intertidal and into the subtidal zone, and has been reported from a diversity of substrates (Kopin et al. 2001). Many authors have stated that a greater habitat breadth has been observed in North American studies and this has been attributed to the very high population densities of American invasive populations, resulting in expansion to non-preferred habitats (Anderson and Epifanio 2009), or to shoreline structural complexity, which Lohrer et al. (2000a) speculated could be higher in North America.

In experiments, Asian shore crabs were attracted to both boulders and artificial shade (Takada 1999). They were also strongly attracted to the shelter provided by fucoid algae (Tyrrell et al. 2006). Low-energy, intertidal, boulder/cobble beaches similar to those described as typical habitat in Japan were inhabited in North America, but the crabs also utilized sand/pebble beaches, mussel beds, rock jetties, and wooden bulkheads and pilings (Gerard et al. 1999; Kraemer et al. 2007). All life stages from juvenile to gravid adults were found on sandy beaches near Delaware Bay (Anderson and Epifanio 2009). Asian shore crabs were collected on submerged aquaculture gear (wire cages containing mesh bags of oysters (*Crassostrea virginica*)), and in an eelgrass (*Zostera marina*) bed with mean shoot density of 224–554 shoots/m^2 (Dealteris et al. 2004). Davis et al. (2005) collected crabs from heavily fouled settling structures suspended from a dock at 0.5 depth in a 2 m depth water column. Asian shore crabs were also present as epifauna of floating cages used for oyster (*Crassostrea virginica*), constructed of PVC pipe and vinyl-coated wire mesh and tied to docks in Delaware Bay (Marenghi and Ozbay 2010; Marenghi et al. 2010).

In Rhode Island, Asian shore crab density and native species richness were highest where both cordgrass (*Spartina alterniflora*) and ribbed mussels (*Geukensia demissa*) were present, relative to experimental treatments where one or both of these foundation species were removed (Altieri et al. 2010). Evaporation rates, substrate temperature, and cobble mobility were all lower inside cordgrass beds than outside among the cobbles. Experimentally mimicking cordgrass effects on solar stress and mussel effects on substrate stability (by experimentally shading and/or stabilizing cobbles outside cordgrass beds) increased the density of crabs, when cobbles were both shaded and stabilized, to numbers very similar to natural cordgrass beds. Survivorship of tethered crabs was over seven times higher in cordgrass (92%) than in cobbles (12%) after 24 h. Dead crabs in both habitats were intact but were either crushed by cobbles or desiccated, and there was no evidence of predation, indicating that survivorship was primarily limited by abiotic stress.

Along the Opal Coast, France (the French side of the Dover Strait), Asian shore crab occurred in large numbers on the rocky shore of the open sea, while its congener *H.*

takanoi (also invasive) was abundant in sheltered harbours (Dauvin et al. 2009a). These species occasionally co-occurred inside harbours. Asian shore crab was abundant under boulders on soft bottoms composed mainly of fine sand and gravel in high hydrodynamic areas. Crabs were found high on the shore and not on the lowest part of the shore. The entire eulittoral zone was colonized, but during spring (April–May), the mid-eulittoral was preferred.

In the Oosterschelde, The Netherlands, Asian shore crab was restricted to western shores where the sediment below boulders was sandy, and not muddy. It was confined to a narrow belt at mid-shore levels, being absent from the lowest part of the intertidal zone (D'Udekem d'Acoz 2006).

Asian shore crabs were present in macrofouling communities in the cooling system of the Vladivostok Heat and Power Plant (Moshchenko and Zvyagintsev 2010). They have also been found on scallop collectors in Amur Bay, Sea of Japan. The collectors were mesh bags attached at 1 m intervals to a 6 mm nylon rope in water 7 m deep. The density of juvenile Asian shore crabs on scallop collectors exposed at 6.5 m for 18 months reached 20 crabs/m^2 (Gabaev et al. 2005). In Taiwan, Asian shore crab was, on average, the ninth most abundant (out of 10) crab species collected by various methods at depths down to 40 m, but was the most abundant at the shallowest depth sampled (10 m) (Tew et al. 2008).

Lohrer et al. (2000b) found that habitat utilization patterns were similar in Tanabe Bay, Japan and in a Long Island Sound site. Asian shore crab was predominantly found on moderately exposed shores in both locations, and was rare or absent in low-energy sites with more protection from waves and current. The uppermost tidal height had the lowest abundance of Asian shore crab, but abundance was evenly distributed among the mid- to low levels. The presence of loose stones on top of the substrate appeared important, as this species was always found beneath stones during daytime low tides and was most abundant where cobble and boulder piles provided structure. It was only present among marsh grasses at sites where cobbles and boulders were scattered among the plant shoots. Lower densities of Asian shore crab were recorded in areas where heavy sedimentary burial of loose stones occurred, and the crab was never found in excavated burrows.

Crab densities in Tanabe Bay, Japan, were significantly related to percent cover of total stones, but only in transects where the species was abundant (Lohrer et al. 2000a). Small stone-size categories (11–63 cm in the longest dimension) were not indicators of crab density. Percent cover of large cobbles and boulders (83–172 cm) was positively correlated with density of crabs, and density could be altered by experimental addition or removal of stones in this size category. Stone size also affected crab size, as large Asian shore crabs were mostly found under large stones. Crabs most likely remained under stones during day-time low tides seeking shelter from thermal stress, desiccation, predation, etc. Vadnais (2005) also found that the density of crabs sheltered beneath intertidal rocks at Charles Island in Milford, CT, increased with the rock surface area.

Habitat use in the intertidal zone varied with the size of the crab, and, in general, the larger crabs were found lower on the shore. In Tanabe Bay, Japan, crabs were significantly larger in the lower intertidal zone than higher on the shore (Lohrer et al. 2000a). Recruits (<8 mm CW) were found only in the upper transect. Mean densities were 4.7 crabs/m^2 in the upper zone and 1.1 crabs/m^2 in the lower zone. In another Japanese study, most ovigerous females were found between lower low tide and higher low tide during spring tide. Most females collected higher on the shore than this zone were not yet mature (Saigusa and Kawagoye 1997). At Crane Neck Point, NY, the crabs inhabited a large vertical range in the intertidal zone, from lower low water to 30 or 40 cm below higher high water (Gerard et al. 1999). All the largest crabs (male CW > 30 mm, females 27–28 mm) were found along the lowest transect in the low intertidal zone during summer and fall. The high elevations were dominated by 10–15 mm crabs; few crabs > 20 mm were found there, and none < 8 mm. Similarly, in June sampling conducted at Rye, NY, small Asian shore crabs were more abundant in the upper intertidal zone compared to lower zones, where large crabs were more abundant (Kraemer et al. 2007).

Subtidal reports of Asian shore crab have become common in North America. Anecdotal accounts by commercial fishermen suggest that the range of Asian shore crab extends into the subtidal environment at Rye, NY (Kraemer et al. 2007). In Long Island Sound, Asian shore crab accounted for 20.8% of all crabs caught in subtidal trap surveys (Gilman 2008). Fouling of Asian shore crab carapaces by bryozoans, mussels, and barnacles was indicative of subtidal sojourns, particularly in winter (McDermott 1998).

However, not all Asian shore crabs moved to subtidal waters in winter, and evidently the pattern of smaller crabs remaining higher on the shore was retained year-round. In Rye, NY, part of the population of Asian shore crab appeared to migrate subtidally in winter, but intertidal populations were dominated by small Asian shore crabs in January, and these were restricted to the lower half of the intertidal zone (Kraemer et al. 2007). Similarly, at Crane Neck Point, NY, crabs were found throughout the intertidal zone during summer and fall, but all crabs disappeared from the high intertidal during winter (Gerard et al. 1999). The onset of seasonal activity (migration back to the intertidal zone from subtidal wintering locations) in western Long Island Sound occurs in mid- to late March (Brousseau and Goldberg 2007).

3.5 PHYSIOLOGICAL TOLERANCES

3.5.1 Temperature

The native range of Asian shore crab encompasses areas with water temperatures approximating 0°C in winter in the north and up to 28°C in summer in the south (Gerard et al. 1999). Corresponding temperatures on the Atlantic coast of North America may be found between Atlantic Canada and Florida (Gerard et al. 1999).

In its native range, Asian shore crab has not been reported in locations where the mean summer sea surface temperature was below 12.6°C (Stephenson et al. 2009). In its

invaded range, trace populations (isolated individuals) have been reported at summer sea surface temperature means as low as 12.5°C. Established populations have not been detected in areas with mean summer sea surface temperature < 15°C. The coldest winter sea surface temperature means in the native and invaded ranges of Asian shore crab are 0.3°C and 2.8°C, respectively (Stephenson et al. 2009).

In Maine, populations were absent from areas with mean summer temperatures cooler than 13 °C (Stephenson et al. 2009). In southern Maine, seasonal population densities were greatest during periods with mean temperatures > 15°C and reproduction (i.e., presence of ovigerous females) corresponded to mean temperatures >12°C. Stephenson and colleagues suggested that the invasion of Asian shore crab has stalled at the terminus of the Gulf of Maine's cold, Eastern Maine Coastal Current. They further speculated that future distribution of Asian shore crab would be limited to the warmer areas of the Maine coast, south and west of Penobscot Bay, and up estuaries that warm every summer. Cold summer temperatures inhibiting reproduction and larval development and survival were considered to be the limiting factor. In its native range, Asian shore crab was found in locations where mean winter sea surface temperatures were more than 2°C colder than at its northern limit in Maine.

Delaney et al. (2008) speculated that Asian shore crab could potentially maintain populations in the cold waters of Maine by living in the subtidal zone year-round.

In New Jersey, crabs were relatively inactive during low temperatures from December through February, seeking shelter from freezing air temperatures deep among the rocks or subtidally. Even at air and water temperatures below 5°C, some crabs were found under intertidal rocks in January, February, and March. The lowest air and water temperatures at which crabs were collected were 0.6 and 0.8°C, respectively (McDermott 1998).

In a study of thermal pollution where temperatures varied between approximately 7°C and 27°C, Asian shore crab was found on settling plates situated both before and after the cooling system of the Vladivostok Heat and Power Plant (Zvyagintsev et al. 2004).

Temperatures under rocks at the upper limit of Asian shore crab distribution at Rye, NY, after 5 h emersion during a warm (28°C) June day reached 41°C by 1400 hrs (Kraemer et al. 2007).

In eastern North America, some researchers have suggested that Asian shore crab has reached its northern limit in the state of Maine (Byers and Pringle 2006; Stephenson et al. 2009).

Stephenson et al. (2009) suggested that the winter conditions of Maine were not limiting to survival. They indicated that the winter conditions of Asian shore crab's native range were 2°C colder than the waters of Maine, reaching mean low sea surface temperatures of 0.3°C, which would be consistent with winter survival throughout much of Atlantic Canada. They attributed the failure of Asian shore crab to extend its distribution (as yet)

north of the terminus of the Gulf of Maine's cold Eastern Maine Coastal Current to cold summer sea surface mean temperatures < 15 °C.

Byers and Pringle (2006) suggested that the populations of Asian shore crab observed near the central coast of Maine, where water temperatures are ~15°C, should be ephemeral. Their model predicted, however, that net larval recruitment would be sufficient to maintain a population at temperatures of 20°C during the reproductive season. If correct, this would suggest that Asian shore crab could potentially establish populations under the temperature regime of the southern Gulf of St. Lawrence, but would be unlikely to establish populations elsewhere in Atlantic Canada, where water temperatures are typically less than 20°C in summer.

Van Guelpen et al. (2005), however, using a bioclimate envelope model based on the temperature conditions in the current distribution of Asian shore crab, estimated that it should be able to expand successfully throughout the Bay of Fundy and along the southern Nova Scotia coast to approximately Halifax. They suggested this expansion was likely since, in addition to appropriate temperatures, the area includes rocky shore habitats and the preferred prey of Asian shore crab. A moderate temperature increase of 2°C in global temperature was predicted, under three different climate change scenarios, to result in an extensive northern range expansion. Under these models, Asian shore crab could occur throughout the Atlantic coast of Nova Scotia, Gulf of St. Lawrence, and parts of Newfoundland and Labrador (Van Guelpen et al. 2005).

3.5.2 Salinity

Most Asian shore crab collections in North America and Japan have been associated with areas of salinity > 30‰, but McDermott (1999) reported crabs at sites in NJ and NY with salinities of 21–26‰, and in Cape Charles VA (lower Chesapeake Bay) and Oregon Inlet NC at salinities of 15–19‰. A laboratory experiment indicated that adult male and female crabs all survived exposure to salinities reduced suddenly from 32‰ to 5–25‰ for 24–199 h. One of the six crabs exposed to 5‰ became sluggish during the 24 h exposure (McDermott 1999).

In laboratory experiments, Asian shore crabs tolerated salinity down to 10‰ for 7 d, but showed significant preference for 20 or 27‰ (Gerard et al. 1999). Survivorship at 10‰ was 95–100% but the crabs did not moult, possibly due to salinity stress.

Watanabe (1982) determined that from 22 to 53‰ (50%–175% seawater), crabs were able to maintain hemolymph concentrations iso-osmotic or slightly hyperosmotic. Acclimation to salinity changes was rapid, suggested as an adaptation to living in a nearshore environment with abrupt salinity changes.

The salinity tolerances of larval Asian shore crabs were more restricted than those of the adults (see Section 3.2).

3.5.3 Oxygen

Asian shore crab was present in the hypoxic or anoxic waters near the port of Sakai-Semboku, Osaka Bay, Japan (Yamochi and Oda 2002). The species persisted, and was a dominant species on 2 of 7 sampling dates, even during a period when values of dissolved oxygen were less than 10%.

3.5.4 Toxicology

Experiments have shown that Asian shore crab, on the whole, was quite tolerant to a variety of toxic substances.

The toxic effect of Puffer Fish (*Fugu rubripes*) tetrodotoxin (TTX) and saxitoxin (a paralytic shellfish toxin) when directly applied to the nerves of Asian shore crab was similar to that on other tested crabs (Yamamori et al. 1992). However, the haemolymph of the Asian shore crab appeared to contain a TTX-antagonizing protein that increased the species' tolerance to this toxin by almost 40-fold.

Asian shore crab was three to five times more resistant to toxicity from synthetic surfactants used to poison red tide algae, than to Puffer Fish (Ono et al. 1998). The polyoxyethylene alkyl esters tested were lauryl ethylene oxide (EO), myristyl EO, oleyl EO, and coconut fatty acid EO (consisting mainly of palmitic, oleic, and linoleic acids).

Asian shore crabs exposed to one of the most polluted areas of Amersky Bay, Sea of Japan, with high levels of nutrients, heavy metals, DDT, and oil hydrocarbons from the domestic and industrial sewage of Vladivostok, were challenged by injecting 1% formaldehyde into the right cheliped (Kotsyuba et al. 2010). Crabs from the control group (from unpolluted Vostok Bay) survived this acute stress better than those from the polluted site. Only 10% of the control crabs died within 4 h after the injection, compared to 60% of the crabs from the polluted site. Crabs from the control group were more likely to shed the damaged cheliped. Autotomy of the cheliped occurred in 80% of the control crabs within the first minute after the injection, whereas autotomy was observed in only 10% of the crabs from the polluted site. The histochemical and immunocytochemical responses of the nitric oxide system of the crabs also differed, indicating that the involvement of nitric oxide in the formation of behavioural defence responses was influenced by pollution.

3.6 BEHAVIOUR

3.6.1 Settlement and Metamorphosis

Settlement and metamorphosis of the megalopae was induced only by a cue found in the exudate from conspecific adults and cues associated with biofilm-covered substratum from natural rocky intertidal habitat (Kopin et al. 2001). Once established, adult crabs produced cues that promote gregarious settlement, but settlement was not facilitated by response to cues produced by native xanthid crabs (Kopin et al. 2001). The cue was highly species-specific (Steinberg et al. 2007).

The percentage of metamorphosis was examined in megalopae caged at intervals along transects extending 20 m from established Asian shore crabs on rocky intertidal habitat, into open water or toward a salt marsh (Anderson and Epifanio 2010b). Around 90% of megalopae underwent metamorphosis in cages located 1–2 m from the rocky intertidal habitat and concentration of adults, and <70% in cages located 20 m from adult habitat. It was suggested that megalopae can sense water-soluble metamorphic cues produced by adults at distances of a few metres from the source.

Experiments on moulting of megalopae placed in cages or jars adjacent to adult habitat (cobble beach) and in a salt marsh 35 m away indicated that waterborne cues for moulting were equally detected in both areas (Anderson and Epifanio 2010b). The moulting of Asian shore crab was considered to be less habitat-specific than that of some native species.

The proteinaceous settlement cue was produced by both adults and juveniles and began to degrade within two days of production (Anderson et al. 2010). The threshold of detection of the cue by megalopae was at concentrations between 0.1 and 0.01 μg of total protein (not the specific metamorphic clue) per ml of water.

3.6.2 Site Fidelity

Asian shore crab, in addition to being a highly mobile species, shows limited fidelity to a particular shelter or feeding site (Brousseau et al. 2002). There was no difference in site fidelity between males and females, but only nongravid females were studied. A conservative estimate (based on recovered crabs only) of the mean distance travelled in 24 h was 7.43 ± 1.54 m. Among those crabs recovered a distance ≥ 5 m from the release point (92% of the recoveries), the mean distance travelled was 16.87 ± 2.23 m. Despite the low site fidelity and high mobility of the species relative to other crab species, Brousseau et al. (2002) estimated the predation rate on Asian shore crab was 12.5%. The predation rate was low in comparison to those determined for other similar-sized crab species (30% to 89% per day) with much higher site fidelity and lower mobility. This result was counterintuitive, considering that high mobility would be expected to increase exposure of crabs to predators. The pattern of bite marks on the carapace of Asian shore crabs that did not escape was consistent with predation by fishes. The authors suggested that Asian shore crab uses crypsis rather than rapid flight to escape predators while travelling.

3.6.3 Competition

In the mid- to upper rocky intertidal zone, Asian shore crab exploited a niche mostly unoccupied by native brachyurans in eastern North America (McDermott 1998). In the northern part of the range there was spatial overlap with the green crab (*Carcinus maenas*). In North Carolina, Asian shore crab co-occurred with another grapsid, the wharf crab (*Armases cinereum*), in the high intertidal zone.

In 1997, Asian shore crab outnumbered all other crab species combined at Greenwich Point, CT (Ahl and Moss 1999).

At Townsend and Hereford Inlets, NJ, green crab encroached onto the upper intertidal Asian shore crab habitat. Seven other brachyurans inhabited the lower third of the intertidal and shallow subtidal zones (McDermott 1998). At low tide periods, Asian shore crabs moved to lower levels to feed, and at those times were found under the rocks together with green crabs and mud crabs (*Panopeus herbstii*).

Flatback mud crab (*Eurypanopeus depressus*) was the most abundant crab in Rye, NY, before the arrival of Asian shore crab and was co-dominant with Asian shore crab during the first years of a study conducted from 1998 to 2005 (Kraemer et al. 2007). Flatback mud crab abundance decreased by about 95% from an initial density of 15 crabs/m^2, during a 3-year period when Asian shore crab abundance increased from 15 crabs/m^2 to 120 crabs/m^2. The Shannon diversity index of crab species in the intertidal community declined by more than an order of magnitude during the study.

Lohrer et al. (2000b) found that of the two crabs that overlapped spatially with Asian shore crab in Long Island Sound, the greatest overlap occurred with green crab. The other species, *Eurypanopeus depressus*, mostly occurred lower in the intertidal zone.

Lohrer and Whitlatch (2002a) reported up to 90% decreases in green crab (*Carcinus maenas*) abundance at intertidal sites in Connecticut following the arrival of the Asian shore crab.

The mud crab (*Dyspanopeus sayi*) was formerly common under intertidal boulders at Crane Neck Point, NY, but, by 1999, had almost completely disappeared at that site, although it still occurred subtidally (Gerard et al. 1999). Since mud crab and Asian shore crab could be held together in small tubs in the laboratory for a week without mortality, competition for habitat was suggested as a more likely explanation of the changed distribution at Crane Neck Point than predation (Gerard et al. 1999).

Jensen et al. (2002) found that adult Asian shore crab was 'overwhelmingly dominant' over juvenile green crab of equal size (14–20 mm CW) when competing for food. The species were approximately equal in finding the bivalve bait first in laboratory trials, and green crabs were quicker at opening the bivalves, but green crabs spent only 15% of the time feeding, while Asian shore crabs spent 84% of the time. Green crabs were less likely to initiate contact with the bait while Asian shore crabs fed than the reverse. In these experiments, 95% of approaches by Asian shore crabs successfully displaced green crabs that were already feeding on the bait, but only 38% of the approaches by green crabs successfully displaced Asian shore crabs from the bait. The displacement by Asian shore crabs did not involve overt aggression or chelae displays on the part of the Asian shore crabs, but the use of the body and legs as a wedge to displace the green crabs. Approaching green crabs were fended off with kicks from the walking legs while the chelae continued to be used for feeding. Naïve green crabs from Maine displayed more persistence than green crabs from Delaware (which co-occurred with Asian shore crabs) (7.08 vs. 1.93 unsuccessful approaches) in their efforts to displace Asian shore crabs from the bait, but there was no difference in the success rate of either group

Only 22% of juvenile (14–20 mm CW) green crab occurred under rocks in areas where Asian shore crab occurred; the remainder were primarily buried in sand immediately adjacent to rocks, or sometimes among dense coverings of *Fucus* spp. on the sides and tops of rocks and concrete slabs, but absent from the undersides which were populated with Asian shore crabs (Jensen et al. 2002). The few green crabs that were present under rocks were usually under ones lacking Asian shore crabs. In these areas, 98% of the Asian shore crabs were found under rocks. In similar habitat in Maine (where Asian shore crab was not found at that time), >97% of the juvenile green crabs were found beneath rocks. Asian shore crabs consistently dominated in laboratory contests for shelter under a single bivalve shell; only 7% of green crabs confined with Asian shore crabs utilized the shell, in contrast to 42% in controls. The presence of green crabs had no effect on shell utilization by Asian shore crabs (Jensen et al. 2002).

Interference between Asian shore crab and green crab reduced the risk of predation for shared amphipod prey (Griffen and Byers 2006).

According to Blakeslee et al. (2009), Asian shore crab has displaced green crab as the most abundant rocky intertidal crab in much of its new range. Asian shore crab was present, on average, at twice the density (and up to 10 times the density) of green crab in the intertidal zone. The two species of crabs co-occurred in the Gulf of Maine, but the densities of green crab in the southern part of the range had declined precipitously, at least in part due to strong interspecific negative interactions between the crabs.

Dauvin (2009b) suggested that competition between Asian shore crab and green crab in its native environment might prevent the Asian shore crab from reaching the extremely high abundances in Europe it had attained in the eastern USA. By 2008, Asian shore crab densities were moderate or low in Belgium and The Netherlands. In Europe, green crab is a native species and its genetics are evidently more variable at the individual and population level than in American populations, which Dauvin suggested was likely to increase its competitive ability.

The habitat of Asian shore crab in France was similar to that of the green crab (Dauvin et al. 2009).

A community-level foraging experiment was conducted in field enclosures in New Hampshire, using Asian shore crab (12–34 mm CW) and green crab (12–55 mm). The combined effects on blue mussel (*Mytilus edulis*) and herbivorous snails (*Littorina littorea* and *L. obtusata*) of Asian shore crab and green crab foraging together were similar to those produced by green crab foraging alone, but the effects of Asian shore crab foraging alone were weaker (Griffen and Byers 2009). In contrast, when both predators foraged together, impacts on barnacles (*Semibalanus balanoides*) (survival increased by ~40%), and brown algae (*Fucus* sp., and *Ascophyllum nodosum*) (biomass increased by ~30%) were reduced relative to those of a single crab species foraging alone. When individual prey types were examined, impact increased with increasing prey densities, but only for the most abundant prey (red algae (*Chondrus crispus*,

Mastocarpus stellatus, and *Polysiphonia lanosa*), and brown algae) and most preferred prey (mussels and, to a lesser extent, barnacles). Consumption of 'drift' red algae also increased with predator density, but was not different between the two crab species. While impacts of predators on most prey types were similar, green crabs had a greater positive impact on brown algae at lower densities. When densities of the two species were compared in a ratio that reflected their abundance in the New Hampshire environment (10 green crabs vs. 40 Asian shore crabs), Asian shore crabs had a 30–50% larger impact across the entire prey community. Impacts of both crabs on barnacles, mussels, and snails were greater in the study year when those prey were more abundant (Griffen and Byers 2009).

Cannibalism was an important factor causing high levels of mortality among the small size class of crabs for both species in the Griffen and Byers (2009) experiments, becoming stronger for both species as predator densities increased. Cannibalism among green crabs remained consistently high over both years at approximately 40% mortality each month; while cannibalism among Asian shore crabs increased from 11% per month in 2005 to 33% in 2006 when other animal prey was less available.

The effects of the green crab and Asian shore crab on the New Hampshire intertidal community were very different in 2005, but were similar in 2006 (Griffen and Byers 2009). Contrary to previous reports of large interference effects of Asian shore crab on green crab foraging, interference between the two species only weakly reduced mortality of barnacles and brown algae, and did not alter impacts on the rest of the prey community. Strong interference effects that reduce mussel mortalities were likely absent here because experiments were sufficiently long that mussel depletion could occur, even at reduced predation rates. The influence of crab density on community impacts of these predators was lower than anticipated, possibly due to cannibalism, and also was lower in years with lower availability of favoured prey.

Interference between green crab (40–60 mm CW) and Asian shore crab (25–33 mm CW), referred to as 'predator interference', was documented by Griffen and Delaney (2007), both when preying on a single focal prey species (*Mytilus edulis*) and when foraging more broadly across the entire prey community. Aggressive interactions among conspecifics are much stronger for green crab than for Asian shore crab. The per capita rate of blue mussel consumption by adult green crab is approximately twice that of Asian shore crab. Preferred sizes of mussel prey differed between crab species: 14–17 mm shell length for green crab, 7–10 mm shell length for Asian shore crab. For green crab, higher densities of conspecifics decreased search efficiency and increased handling time of prey. For Asian shore crab, prey handling time increased at higher conspecific densities, but search efficiency was not affected. Replacement of green crab by Asian shore crab thus shifts predation from a species that experiences strong predator interference to one that experiences weaker predator interference. In other words, green crab populations are more self-limiting at high levels of abundance than are those of Asian shore crab. In addition to the high level of predation interference that occurs at high densities of green crab, Griffen and Delaney (2007) noted a high

occurrence of cannibalism in such populations. Griffen and Byers (2009) found cannibalism rates to be lower in Asian shore crab than in green crab.

Population density of Asian shore crab was greater than that of green crab in the region south of Cape Cod. At sites in the Gulf of Maine, where both species were present, they were found in similar densities (Griffen and Delaney 2007). In New Hampshire (Gulf of Maine), Asian shore crab densities were 10% of those of green crab for the first few years following its arrival (Tyrrell et al. 2006).

Griffen et al. (2008), investigated the interactions between the green crab and the Asian shore crab through a series of field (within the Gulf of Maine) and laboratory investigations. They found that density patterns of green crabs and Asian shore crabs at different spatial scales were consistent with negative interactions. As a result of these interactions, green crab altered its diet in the presence of Asian shore crab. Overall, green crab consumed less food when Asian shore crab was present. It consumed fewer mussels and amphipods and consumed more red algae when Asian shore crab was present. Growth rates for green crab were reduced, with potential detrimental effects on green crab populations (Griffen et al. 2008). In contrast, Asian shore crab did not alter the amount of food it consumed, or the content of its diet, when green crab was present.

Reduced mussel consumption by green crab in the presence of Asian shore crab might not reflect exploitative competition for a limited resource, as mussel density was high at multiple sites where consumption of mussels by green crabs was low (Griffen et al. 2008). Rather, it might reflect displacement of green crabs from prey by Asian shore crabs, or potentially reflect a 'hardwired' behavioural response to high densities of any competing individuals.

Aggressive interactions between green crabs and Asian shore crabs increased with density, but did not increase as fast as negative interactions between conspecifics (Griffen and Williamson 2008). At low density, interactions between conspecific and heterospecific predators had similar inhibitory impacts on predator function, whereas conspecific interference was greater than interference from heterospecifics at high predator density. Prey (blue mussels of 15–20 mm shell length) survival was greater than expected based on the additive model (i.e., risk reduction occurred) for the two lowest predator densities, but at the two highest predator densities, prey survival was not different from expected based on the additive model, indicating that at high densities the two species had independent effects. The mussels used in this experiment were the preferred size for green crab, i.e., larger than the preferred prey of Asian shore crab, but within the range of mussels consumed by Asian shore crab. Experiments were conducted at Odiorne Point, NH, where densities of large Asian shore crabs (>20 mm CW) ranged from 0 to 16 crabs/m^2, green crabs (>30 mm CW) ranged from 0 to 16 crabs/m^2, and mussels were present in the intertidal region at 198 ±197 mussels/m^2.

Over a 4-year period in the late 1990s, Lohrer and Whitlatch (2002b) documented a 40–90% decline in green crab abundance, and a 10-fold increase in Asian shore crab at

three sites in southern New England. Small, newly recruited green crabs had a significant risk of predation when paired with larger Asian shore crabs in the laboratory, and recruitment of age-0 green crabs was reduced through predation by Asian shore crabs as well as through cannibalism by larger conspecifics. In contrast, recruitment of age-0 Asian shore crabs was not affected by larger individuals of larger crab species (Lohrer and Whitlatch 2002b).

From 1996 to 1999, density of Asian shore crab increased substantially in cobble habitats in Connecticut and Rhode Island (Lohrer and Whitlatch 2002b). By August 1999, at two of the sites, densities of Asian shore crabs averaged >70 crabs/m^2, while green crab densities were near zero. Green crabs >10 mm CW were only common at a third site, where densities of larger Asian shore crabs were <40 crabs/m^2. In experiments, when the Asian shore crab was 10 mm larger than the green crab, there was a 50–80% chance that the Asian shore crab would consume the smaller green crab. Green crabs with the same size advantage had a 10–40% chance of consuming smaller Asian shore crab. At carapace width differentials > 20 mm, the probability of predatory activity approached 100% for both species.

Predation on settling green crabs in the intertidal zone may have been a minor constraint on recruitment before the arrival of the Asian shore crab (Lohrer and Whitlatch 2002b). Green crabs that settled one year had usually grown >35 mm CW by the next year's recruitment season (late summer/early fall) and then usually left the intertidal habitats they settled in to adopt a subtidal or tidal migratory lifestyle.

Lohrer et al. (2000b) conducted habitat, spatial, and diet studies on Asian shore crab in its native and invaded (Long Island Sound) habitats, and determined that the resource use of Asian shore crab was quite different from that of other resident species in its invaded habitat. Diet overlap studies were limited to numerically dominant species co-occurring with Asian shore crab in Long Island Sound: green crab, and the native xanthid, *Eurypanopeus depressus*. These three taxa made up >99% of the crabs sampled. Occasionally, *Cancer borealis*, *C. irroratus*, and *Panopeus herbstii* co-occurred with Asian shore crab. Potential competitors in the American habitat were few, compared to Tanabe Bay, Japan, where 11 crab species (many of them in the same subfamily and at least one congener) co-occurred in the same sampled quadrats with Asian shore crab.

MacDonald et al. (2007) noted some spatial overlap between blue crab (*Callinectes sapidus*) and Asian shore crab, which were found in the same marsh area, in the vicinity of a mussel bed at Union Beach, NJ. They inferred competition for space might occur, given that both species were found in areas with sand and stones. Asian shore crab occasionally occupied fiddler crab burrows in *Spartina* marshes (Brousseau et al. 2003), a habitat often used at high tide by foraging blue crabs. Based on food competition experiments for ribbed mussel (*Geukensia demissa*) and Silverside (*Menidia menidia*), MacDonald et al. (2007) concluded that Asian shore crabs and blue crabs of similar size were evenly matched. Given the limited overlap between the two species, competition with Asian shore crab was unlikely to have a large impact on blue crab.

Macdonald et al. (2007) conducted experiments to test for interactions between the blue crab and invasive crabs, using juvenile male blue crabs, green crabs, and Asian shore crabs. Green crabs were more likely to encounter the food, and to consume the food, within the trial time (30 min) than either of the other species. The authors also noted 'severe' predation pressure on green crabs, and potentially on Asian shore crabs, in areas where they co-occurred with adult blue crabs. It was suggested that the displacement of green crabs from rocky shores and jetties by Asian shore crab had the effect of forcing green crabs into habitat where they were vulnerable to predation by adult blue crab, thus reducing competition between green crabs and juvenile blue crabs. However, in areas where adult blue crab abundance was low, such as on the periphery of its range, corresponding to areas where green crab and Asian shore crab are abundant, its juvenile recruitment could be affected by the presence of these two competitors.

In microcosms, green crab and Asian shore crab were found to have similar consumption patterns, causing significant declines in barnacles (*Semibalanus balanoides*), juvenile mussels (*Mytilus edulis*), polychaetes (*Spirorbis* sp.) and ephemeral algae (Tyrrell et al. 2006). In 2-day and 14-day experiments, the decline in *S. balanoides* in the Asian shore crab treatments was greater than that in the green crab treatments, suggesting that the per capita impact on barnacles of Asian shore crab was greater than that of green crab.

3.6.4 Other

When Asian shore crabs were placed into experimental tanks without sediment, the crabs were occasionally observed to cling to each other in a ball formation, appearing to be using each other as shelter. This aggregative behaviour was not observed in megalopae or stage I post-settled crabs (Kim and O'Connor 2007).

3.7 DIET AND FEEDING

The results of diet and feeding studies are context-dependent and sometimes appear to be inconsistent with one another. This is inevitable, given that diets are influenced by factors such as the abundance and composition of potential food items in the environment, prior feeding experience, the presence of competitors, and the physiological state of the crab. However, it is clear from the studies summarized here, that the Asian shore crab is a generalist omnivore with the capacity to consume a wide range of prey, primarily molluscs, crustaceans, polychaetes, and algae.

In both native (Japan) and invaded (Long Island Sound) habitats, Asian shore crabs consumed turf-forming red algae, green sheet-like algae, mytilid bivalves, small herbivorous snails, small crustaceans, and polychaetes (Lohrer et al. 2000b). Both male and female crabs generally consumed calcified prey items that were small in size (snails < 4 mm shell height, mussels < 10 cm shell length). Barnacles (*Semibalanus balanoides*) were consumed in the invaded habitat only. Plant material (green, brown, and red algae, and vascular plant (*Zostera marina*) debris) made up the largest portion of the overall diet of Asian shore crab in both native and invaded habitats. Animal food

items made up ~40% of the overall diet. Crabs collected in Long Island Sound had more animal food in their diet than those collected in Japan (Lohrer et al. 2000b).

Brousseau and Baglivo (2005) found that the Asian shore crab (12–20 mm CW) was an opportunistic omnivore with a strong preference for animal items over algae. In laboratory experiments, 71% of crabs given a choice between macroalgae (*Enteromorpha* spp., *Chondrus crispus*) and benthic invertebrates (*Mytilus edulis, Semibalanus balanoides*) consumed animals only, even when the likelihood of encountering macroalgae was three times as great as that of encountering animal prey. Of those crabs preferring animal food, 90% ate mussels only, none ate barnacles only. There were no significant differences in food preference between sexes or between juvenile and adult crabs. Crabs starved for 5 days consumed both food types more often than crabs starved for 1 day. Increased crab density also led to increased diet breadth.

In Long Island Sound, 86% of Asian shore crabs had consumed food before capture (Brousseau and Goldberg 2007). Food items included the barnacle *Semibalanus balanoides*, detritus, macroalgae, and juvenile polychaete worms. Cypris larvae were found in 43.5% of crab stomachs sampled in April. Crushed barnacle shells were found in at least 45% of crabs from mid-April to mid-June. By the end of May, the numbers of crabs feeding on green algae increased to >80%.

Asian shore crabs readily consumed juvenile snails (*Littorina littorea*) of 8 to 13 mm in height and blue mussels (*Mytilus edulis*) of 9 to 20 mm in length (Gerard et al. 1999). Newly recruited littorines and mussels would require 4–12 months to reach sizes that are too large to be eaten. Other diet items included macroalgae (*Ascophyllum nodosum, Fucus spiralis, Chondrus crispus*), barnacle (*Semibalanus balanoides*), amphipod (*Gammarus* sp.), and newly moulted conspecifics. The only organisms not used as food were mud crabs (*Dyspanopeus sayi*) of similar size (20–27 mm). Individual Asian shore crabs (24–27 mm CW) consumed a daily average of 11.5 juvenile snails, 6.8 juvenile mussels, or 0.1 g of *Ulva lactuca*.

All sizes of male Asian shore crabs of 12–32 mm CW consumed blue mussels of 4–8 mm shell length, when presented with mussels of 4–24 mm. Even crabs >18 mm ate the smaller mussels in preference to those of 12–16 mm; no mussels in the size category 20–24 mm were consumed (Bourdeau and O'Connor 2003). All sizes of male crab ate clams (*Mercenaria mercenaria*) from the smallest size class, 4–8 mm. Only male crabs ≥26 mm CW ate clams larger than 6 mm. In a separate 'critical prey size' experiment, the largest mussel and clam opened and consumed (31 and 17 mm, respectively) were attacked by males of 32.6 and 30.5 mm CW, respectively. Female crabs (same size range as the males) presented with mussels ate small prey (4–8 mm) almost exclusively. Female crabs did not attempt to open any clams, but consumed all the flesh when offered opened clams. Periwinkles (*Littorina littorea*) were not effectively consumed by either male or female crabs. Only 7 small (2–4 mm shell height) periwinkles were consumed by 24 male crabs offered 180 snails of 2–12 mm shell height. These snails were not crushed outright, but opened through breakage of the

aperture. Many unsuccessful attempts at opening snails, in the form of clipped aperture edges and shredded operculum were observed. It is possible that the immobilization of snails in this trial, which caused them to withdraw their operculum deep within the shell, may have restricted the crab's ability to open the snails. Females did not consume snails.

Large (26–23 mm CW) male crabs presented with equal numbers of mussels and clams consumed both species equally (Bourdeau and O'Connor 2003). Female crabs consumed only mussels. Overall, it was concluded that mussels were more vulnerable than clams to Asian shore crab predation. In addition to refuge from predation at smaller sizes (due to their thicker shell), clams typically occur in sandy and muddy regions of the intertidal zone, which is not preferred habitat for the crabs (Bourdeau and O'Connor 2003).

Asian shore crabs exhibited variable shell opening tactics for bivalves (Bourdeau and O'Connor 2003). Smaller bivalves were crushed. Larger bivalves were opened by a variety of techniques including: umbo crushing, where force was applied to the umbo end of the shell; posterior crushing, in which force was applied across the valve plane at the posterior end of the shell; and edge clipping, involving the application of force to the perimeter of the posterior end of the shell with minimal shell damage. The umbo was the most frequently broken shell region of larger prey.

Crabs offered small (4–8 mm) mussels and green algae simultaneously showed no clear preference for mollusc or algal prey (Bourdeau and O'Connor 2003). In algal preference experiments, male and female crabs (12–32 mm CW) preferred *Codium fragile tomentosoides* and *Enteromorpha* spp. and consumed little or no *Chondrus crispus*, *Fucus* spp., and *Ascophyllum nodosum* (Bourdeau and O'Connor 2003). This contrasts with the results of Griffen et al. (2008) who found that *Chondrus crispus* was frequently found in the guts of field-collected crabs and was preferred in feeding trials. Similarly, *Codium* (although found to be a preferred food by Bourdeau and O'Connor (2003)) was rarely found in the guts of crabs in the field (Ledesma and O'Connor 2001; Lohrer and Whitlatch 1997).

Forty-two percent of Asian shore crabs sampled from Connecticut and Rhode Island were missing at least one limb, which affected feeding rate and choice of prey (Davis et al. 2005). Larger crabs were missing more limbs than smaller crabs. Sixteen percent of the crabs were missing at least one cheliped, and chelipeds were more likely to be lost than walking legs. Male crabs missing one cheliped fed slower than those with both chelipeds, but consumed a similar ratio of small to large prey. One-clawed crabs of 36 mm CW fed at about the same rate as two-clawed crabs of 23 mm CW. Crabs with no chelipeds fed at 17% the rate of one-clawed crabs and 13% the rate of two-clawed crabs, and consumed a larger ratio of small to large prey.

Stomach and fecal analysis and laboratory observations showed that Asian shore crabs fed on diatoms, green algae, *Mytilus edulis*, *Semibalanus balanoides*, amphipods and isopods (McDermott 1998).

Both male (10.5–18 mm CW) and female (13.8–17.3 mm CW) Asian shore crabs preyed heavily on *Crepidula fornicata* juveniles. The crabs ate an average of 4 out of 5 *C. fornicata* juveniles one day after the juveniles had metamorphosed. Levels of predation on the juveniles increased significantly on larger snails, 10 days post-metamorphosis (Pechenik et al. 2010).

While adult green crabs were larger than Asian shore crabs and were immune to predation by Asian shore crabs, 99% of the green crabs sampled in rocky intertidal areas were smaller than the maximum size of Asian shore crabs (Lohrer 2000). In field experiments, densities of green crab < 10 mm CW were reduced by interspecific predation.

Grazing mollusc species eaten by Asian shore crabs in New England included the limpet *Notoacmea testudinalis*, the chiton *Tonicella rubra*, the bivalve *Anomia simplex*, and the snails *Littorina obtusata* and *Lacuna vincta* (Tyrrell et al. 2006). The polychaete *Spirorbis* sp. was reduced in abundance by crab grazing, as were the barnacle *Semibalanus balanoides*, and ephemeral algae (this category included *Scytosiphon lomentaria*, *Rhizoclonium tortuosum*, *Chaetomorpha* sp., *Ulothrix flacca*, *Cladophora* sp., *Enteromorpha* sp., *Porphyra* sp., *Dumontia contorta*, and diatoms). Two other algal categories increased in crab treatments compared to controls: algal crust, and fucoid algae (*Fucus vesiculosus* and *Ascophyllum nodosum*). Asian shore crab also fed on mussels *Mytilus edulis*, selectively eating mussels < 10 mm. There was no difference in size frequency distribution of *Littorina littorea* due to predation, although the crabs fed on this species also. High levels of predation on the barnacle *S. balanoides*, which is an important food source for the intertidal predatory snail *Nucella lapillus*, could lead to competition for food with *N. lapillus*. Trussell et al. (2003) have further noted that cues indicating increased risks of predation by crabs lower the feeding rates of *N. lapillus* on *S. balanoides*. An additional impact of the removal of barnacles is that the physical structure of barnacle tests provides heterogeneity that enhances the recruitment and survival of algae and animals.

Abundance of brown algae (*Fucus* sp. and *Ascophyllum nodosum*) increased in treatments with Asian shore crabs compared to control treatments, most likely due to positive indirect effects of crabs on algae through reduction of snail abundance and/or foraging (Griffen and Byers 2009).

Chondrus crispus was frequently found in guts of field-captured Asian shore crabs in the Gulf of Maine and was favoured by Asian shore crabs over other species of macroalgae in feeding trials (Griffen et al. 2008).

There was a strong, but not statistically significant, trend of decreasing percentage cover of algae (*Ulva* sp.) on settling plates in relation to higher crab density (treatments were 60, 180, and 360 crabs/m^2) in Long Island Sound (Brousseau and Goldberg 2007). This was probably caused by increased grazing activity (Brousseau and Goldberg 2007).

In Rye, NY, lower intertidal density of the common periwinkle *Littorina littorea* decreased by about 80% concurrent with the expansion of the Asian shore crab population, which reached 120 crabs/m^2 and then declined to 80 crabs/m^2 (Kraemer et al. 2007).

Asian shore crab reduced *N. lapillus* predation on barnacles *Semibalanus balanoides*, although its effect was weaker than that of green crab (Griffen and Byers 2009). Indirect effects of crabs on barnacles were only apparent in a year when the majority of *N. lapillus* were small, and thus more vulnerable to crab predation.

Experiments with male crabs of 24 mm (±3 mm) CW, at densities of 1 or 2 crabs in an enclosure of 0.6 x 0.5 m, on mussels of 10–20 mm shell length found that in 6 days at mussel densities of 133 and 267 mussels/m^2, 25–30% of the prey was consumed by Asian shore crabs (Griffen 2006). Green crabs consumed approximately 50% more mussels than Asian shore crabs. Alternative prey were available in the field enclosures.

DeGraaf and Tyrell (2004) found that male Asian shore crabs (22.5 mm CW, 5.2 g) had a larger per capita impact on prey populations than green crabs (26.4 mm CW, 4.6 g). Asian shore crabs and green crabs had similar feeding rates on blue mussels 4.5–5.5 mm (~17 mussels/8 hr trial). Asian shore crabs had significantly higher feeding rates on larger size classes of mussels (~16 mussels of 9.5–10.5 mm and ~11 mussels of 14.5–21.5 mm). It was suggested that Asian crab might be a more important bivalve predator than green crab in Long Island Sound, because of its exceptionally high densities (Lohrer and Whitlatch 2002a; Brousseau and Baglivo 2005).

In Europe, the main concern indicated was the potential for threat to aquaculture of *Mytilus edulis* and *Crassostrea gigas* along the French Atlantic coast (Dauvin 2009b). As of 2009, a single observation indicated the presence of Asian shore crab within a mussel farm in the north of the Bay of Somme, in the eastern part of the English Channel (Dauvin 2009b).

Southern New England mussels (*Mytilus edulis*) expressed inducible shell thickening when exposed to waterborne cues from Asian shore crabs (Freeman and Byers 2006). Naïve northern mussel populations from Maine (which had not been invaded at that time) did not respond.

Percentage contribution of mussels to Asian shore crab diet increased with higher mussel density. Across all sites, 9% (±3%) of the Asian shore crab diet was composed of mussels, compared to green crab at 30% (±8%) (Griffen et al. 2008). There was no influence of crab size on percentage contribution of mussels to the diet within the range of crab sizes examined (18–35 mm CW).

Asian shore crab readily consumed Cypris larvae and early post-settlement juveniles of the barnacle *Semibalanus balanoides* in western Long Island Sound (Brousseau and Goldberg 2007). Crab predation did not affect barnacle recruitment when predator density was low (60 crabs/m^2). Barnacle density was reduced at medium (180

crabs/m^2) and high (360 crabs/m^2) predator density immediately after the larval settlement period had ended, but this effect was short-lived. By the end of July, fewer than 20% of crabs had barnacles in their diet. The authors concluded that crab predation had no significant effect on the recruitment success of *S. balanoides* populations.

Under some conditions, Asian shore crab reduced predation by the whelk *Nucella lapillus* on barnacles (*Semibalanus balanoides*), although its predatory effect was weaker than that of green crab (Griffen and Byers 2009). Indirect effects of crabs on barnacles were only apparent in 2005, when the majority of *N. lapillus* were small and thus more vulnerable to crab predation. While Asian shore crab had positive indirect effects on barnacle survival, these were overshadowed by strong direct negative effects of direct barnacle consumption.

Amphipods were present in the guts of 22% of Asian shore crabs (McDermott 1998).

3.8 PARASITES

There appeared to be no overlap in parasites between Asian shore crabs in the USA and Asia. Average parasite richness for Asian sites was1.57 (± SE 0.30), and for American sites was 0.33 (± 0.20), a significant reduction in diversity in the invaded range (Blakeslee et al. 2009). In Japan, recorded Asian shore crab parasites included: an unidentified microsporan, two rhizocephalans (*Polyascus (=Sacculina) polygenea, Sacculina senta*), and three trematodes (*Maritrema setoensis, Microphalloides japonicus, Macrophallus (=Probolocoryphe) asadai*). *P. polygenea* was also recorded in Russia. In the introduced range, only unidentified larval nematodes have been found: in Connecticut, New York State, Delaware, and Maryland (Blakeslee et al. 2009). The nematode was limited to the southern areas of the American range (Rye, NY, and more southern sites).

On the whole, parasite prevalence in the introduced US range was about 90% lower than the native range (Blakeslee et al. 2009). In Asia, the overall parasite prevalence was 4% for castrating parasites and 58% for trophically transmitted parasites (Blakeslee et al. 2009). In the USA, prevalence was 0% for castrating parasites and 6% for trophically transmitted parasites. Prevalence of microsporans was 0% in six sites in Japan and 30% in one other site, rhizocephalans were found at three sites where prevalence was 5%, 8%, and 20%, and trematodes were found at all seven sites with mean prevalence of 46.3% (range 15–87%). In the eastern USA, nematodes were found at three of seven sites, with prevalence of parasite infection of 11%, 15%, and 18%.

At Vostok Bay, Sea of Japan, more than 80% of crabs were infested by the rhizocephalan *Polyascus* (*Sacculina*) *polygenea* (Isaeva et al. 2001). Parasitism may have made the crabs more vulnerable to epibionts, presumably due to changes in the crab's ability to rid itself of epibionts. Six of the 47 sacculinized crabs had small bivalve molluscs attached to the ventral side of the thorax or abdomen: nine *Mytilus trossulus* and one *Hiatella arctica*. Epizoans were never found attached to unsacculinized crabs

(~200 specimens were examined). During the period of *P. polygenea* reproduction, host grooming behaviour was reduced.

The larval development of *Polyascus* (*Sacculina*) *polygenea* was comprised of five naupliar stages and a cyprid stage (Kashenko and Korn 2002). Nauplii successfully developed at 18–25°C and 18–34 ‰, reaching the cyprid stage after 2–3 days. Cyprids tolerated a wider salinity range of 8–34 ‰ and survived 6–10 d.

In Vostok Bay, Sea of Japan, externae of *Polyascus polygenea* usually appeared on the surface of the Asian shore crab host at the time when the crab attained sexual maturity (14–15 mm CW) (Korn et al. 2005). More often the infested crabs were 25–29 mm CW. There was no effect of sex of the host on the level of infestation. In summer, the proportion of infested crabs ranged from 7–84%. The largest proportion of infested crabs was found in an area with boulder-pebble substrate and small surf waves.

In Japan, the Asian shore crab is often heavily infested with the rhizocephalan barnacle *Sacculina polygenea* (Takahashi and Lützen 1998). In a low-prevalence locality, prevalence was 1.1–1.7% and the number of internal tumours (primordial parasites) varied from 10–92 tumours/crab. In a high-prevalence locality, prevalence was 41.6–79.6% and there were 20–71 tumours/crab. The parasites generally become external in crabs 1.5–2 years old. Externae die and are replaced 1–3 times during the life of a crab, the host moulting and growing between replacements with concomitant increases in the average number and size of the externae.

The annual growth rate of Asian shore crabs parasitized by the rhizocephalan *Sacculina senta* was about half that of unparasitized crabs (Takahashi and Matsuura 1994). After the release of several broods of larvae, the externa of the parasite detached from the host. Subsequent moulting occurred within 40 days in about 80% of the crabs, but in the remainder it was delayed for up to 4 months. Soon after moulting, a new externa developed on every crab. Many of the infected male crabs were feminized in appearance, having a wider abdomen and smaller chelipeds than unparasitized males.

A new species of digenean, *Maritrema jebuensis*, was described from its intermediate host, the Asian shore crab, in Korea by Chung et al. (2010). The final host of this species is presumed to be a bird.

3.9 EPIBIONTS

In total, thirteen taxa of ectosymbionts have been recorded from Asian shore crab in the USA and the western Pacific (McDermott 2007). Blue mussel (*Mytilus edulis*) spat, and the encrusting, cheilostome bryozoan *Conopeum tenuissimum* were the dominant ectosymbionts of Asian shore crabs from New Jersey, with prevalences of 22.2% and 32.1%, respectively (McDermott 2007). Ranges of intensity were 1–146 spat/crab and 1–31 colonies/crab. Larger crabs had higher prevalences and intensities of *C. tenuissimum* colonies. The encrusting, ctenostome bryozoan *Alcyonidium albescens* was much less common with a prevalence of 3.4%. Other epibionts were the encrusting, cheilostome bryozoan *Membranipora tenuis;* the tubicolous polychaetes

Hydroides dianthus, *Sabellaria vulgaris* and *Spirorbis* sp.; the barnacles *Balanus improvisus* and *Semibalanus balanoides*; and unidentified thecate hydroids (McDermott 2007).

As noted in the preceding section, the presence of parasites such as rhizocephalans may increase infestation by epibionts because of changes in crab behaviour (Isaeva et al. 2001).

3.10 PREDATION ON ASIAN SHORE CRAB

McDermott (Gerard et al. 1999) cited the successful use of Asian shore crab as bait for Tautog (*Tautoga onitis*) in Long Island Sound. A trial in Great South Bay, New Hampshire, found that Asian shore crab was comparable to commercially sold green crabs and fiddler crabs as bait. Gerard et al. (1999) predicted that Asian shore crab would become prey for finfishes that forage in nearshore rocky habitats, including Tautog, Cunner (*Tautogolabrus adspersus*), Striped Bass (*Morone saxatilis*), and Black Sea Bass (*Centropristis striata*). Green crab (*Carcinus maenas*), native rock crab (*C. borealis)*, herring gulls (*Larus argentatus*), and black-backed gulls (*L. marinus*) are also potential predators of Asian shore crab.

Fishermen at Townsends Inlet, New Jersey, were using Asian shore crabs from underneath the higher intertidal rocks for bait for unspecified fishes by 1998 (McDermott 1998).

Striped Killifish (*Fundulus majalis*) readily preyed on Asian shore crab megalopae and newly-settled crabs in the laboratory (Kim and O'Connor 2007). Megalopae lacked chemical or morphological defences. Almost all newly-settled 1st-stage crabs were consumed in the laboratory in the absence of shelter but only about 30% were eaten by killifish when sediment consisting of rocks and sand was present. Killifish generally failed to consume crabs of >= 3 mm CW regardless of whether shelter was present. No crabs were found in the guts of wild-collected killifish but very few crabs < 5 mm were present around the time of sampling. Another explanation for the lack of wild-consumed crabs might be that killifish were visual (diurnal) predators and crabs might only be active at night.

In western Long Island Sound (CT), only 13% of Common Mummichog (*Fundulus heteroclitus*) and 7.7% of Striped Killifish (*F. majalis*) with food in their guts had ingested Asian shore crab (Brousseau et al. 2008). Of these fishes, one-third had consumed whole crabs. The rest had only autotomized appendages in their guts. In spite of the addition of an abundant new food item, there was no evidence that food selection patterns of either *Fundulus* species had become less generalized or had shifted to include more crabs over the 4-year study period. The presence of just appendages in the majority of crab-eating fishes suggests that Asian shore crabs could successfully evade predation by autotomizing limbs. The high numbers of Asian shore crabs with missing limbs present in many populations (Brousseau et al. 2008; Davis et al. 2005) suggests that the benefits associated with autotomy outweigh the loss of feeding efficiency. The mean carapace width of juvenile crabs ingested by Mummichog was

3.59 (± 2.22) mm. A size refuge from killifish predation would be reached at approximately 40 days post-settlement.

A pilot study of juvenile Tautog found Asian shore crab in <1% of guts, although small mud crabs were present in ~50% of guts (Kim and O'Connor 2007).

In its native habitat, Asian shore crab was consumed by the sculpins *Myoxocephalus stelleri* and *M. brandti* (Pushchina and Panchenko (2002), as cited in Kim and O'Connor 2007).

The chelipeds of a decaying Asian shore crab were readily consumed by the nemertean *Tortus tokmakovae*, although nemerteans kept in an aquarium for a month with a living juvenile Asian shore crab (5–6 mm CW) did not attack it (Chernyshev 2000).

Diet analysis indicated that Asian shore crab was often consumed by fishes in a Long Island Sound subtidal community. Asian shore crab was found in the guts of 17% of examined Black Sea Bass (*Centropristis striata*), 14% of Tautog (*Tautoga onitis*), 5% of Cunner (*Tautogolabrus adspersus*), 25% of Oyster Toadfish (*Opsanus tau*), and 0% of Striped Bass (*Morone saxatilis*) (Gilman 2008).

In the northwestern Pacific, Asian shore crab is consumed by the Alaska Greenling (*Hexagrammos octogrammus*) (Pushchina and Antonenko 2000).

4 DISPERSAL CAPABILITIES

4.1 NATURAL DISPERSAL

A relationship that determines if a coastal species with a benthic adult stage and planktonic larvae can be retained within its range and invade in the direction opposite that of the mean current experienced by the larvae ('upstream') was applied to Asian shore crab, assuming per capita fecundity of 200,000–300,000 eggs/yr (Byers and Pringle 2006). About 0.02% net larval survival in a single year would allow retention in 25°C water. For 20°C water, 0.08% net larval survival would be needed. These net larval recruitment rates were well within laboratory-based mortality rates. This was presented as an explanation of how Asian shore crab had been able to expand rapidly hundreds of km 'upstream' (northward against the prevailing southerly current) from its initial discovery in New Jersey. However, for 15°C water, the necessary recruitment rate, even at 100% survival, exceeded the number of larvae a female would be expected to release in two years, suggesting that, in the central coast of Maine where water temperatures are 15°C, Asian shore crab populations should be ephemeral.

4.2 ANTHROPOGENIC DISPERSAL

The likely means of anthropogenic dispersal were shipping vectors. Suggested vectors included ballast water transport of the larvae (McDermott 1998; Breton et al. 2002) and yacht transport of adults or juveniles through hull fouling (Micu et al. 2010).

4.3 POPULATION GROWTH AND ABUNDANCE

Peak population densities in North America (>300 crabs/m^2) were substantially higher than those reported from the native range (~100 crabs/m^2) (Table 4 and Table 5). Once established in a new location, the species has shown the capacity to rapidly expand the population within a few years.

Table 4. Population densities of Asian shore crab in native range

Site	Crab abundance	Reference
Tanabe Bay, Honshu, Japan	Max. density ~55 crabs/m^2	Fukui 1988
Oshoro Bay, Hokkaido, Japan	Max. density ~100 crabs/m^2	Takahashi et al. 1985
Southern Hokkaido, Japan	0.5 crabs/m^2	Fuji and Nomura 1990

Table 5. Population abundances of Asian shore crab in introduced range

Site *	Year of first report	Year for which abundance is reported	No. of years since discovery	Crab abundance	Reference
Townsends Inlet, Cape May, NJ	1988	1988	0	1 crab in total	McDermott 1998
		1996	8	>320 crabs/m^2	
Rye, NY	1994	1998–99	4–5	15 crabs/m^2	Kraemer et al. 2007
		2000	6	60 crabs/m^2	
		2001–02	7–8	120 crabs/m^2 (max. 305 crabs/m^2)	
		2003–05	9–11	80 crabs/m^2	
Southern and western Long Island Sound, NY		2000		Large settlement pulse of juveniles reported	Kraemer et al. 2007
Black Rock Harbour, Bridgeport, CT		2003–05		40 crabs/m^2	Brousseau and Goldberg 2007
Greenwich Pt., CT		1997		22.8 crabs/m^2	Ahl and Moss 1999
Eastern Cotentin coast, France	2008	2008	0	11–12 crabs/m^2	Dauvin 2009b
		2009	1	>50/m^2 at 2 sites	
Opal coast, France	2005	2008	3	0.7–12.0 crabs/m^2	Dauvin et al. 2009
NY (all sites)				2.11–43.83 crabs/m^2	Delaney et al. (2008)
CT (all sites)				18.25–28.25 crabs/m^2	
RI (all sites)				1.26–2.06 crabs/m^2	
MA (all sites)				.28–31.65 crabs/m^2	
NH (all sites)				0.09–2.86 crabs/m^2	
ME (all sites)				0–0.19 crabs/m^2	
New Haven, CT				2.6 to 5.6 crabs/m^2	Lohrer and Whitlatch 1997
Hammonasset, CT				17.9 crabs/m^2	
Crane Neck Point, CT		1997–98		7.1 to 10.3 crabs/m^2	Gerard et al. 1999

Site *	Year of first report	Year for which abundance is reported	No. of years since discovery	Crab abundance	Reference
Millstone Point, Eastern Long Island Sound				Max. density > 150 crabs/m^2	Lohrer and Whitlatch 2002a
Demerest Lloyd State Park, MA				Max. density under rocks 190 crabs/m^2	Jensen et al. 2002
South Odiorne Point, NH				mean 3.6 crabs/m^2 (range 0–38 crabs/m^2)	Griffen 2006

*CT (Connecticut); MA (Massachusetts); ME (Maine); NH (New Hampshire) NJ (New Jersey); NY (New York State); RI (Rhode Island)

5 SUMMARY

The Asian shore crab is native to Sakhalin Island (Russia), Korea, Japan, North China, Hong Kong, and Taiwan. As of December, 2011, Asian shore crab has not been reported from Canada. It has established, however, in the northwestern and northeastern Atlantic Ocean. It was discovered in New Jersey in 1988 and has subsequently developed well established populations from North Carolina to central Maine. The first European specimens were observed in The Netherlands in 2003. Asian shore crab has now established populations in the northeastern Atlantic from the west coast of the Cotentin Peninsula, France, in the English Channel, to the Lower Saxony state of Schleswig-Holstein, Germany, and has been reported from the Black Sea and northern Adriatic Sea. Natural dispersal is by means of planktonic larvae and benthic adults and juveniles. Shipping vectors, including ballast water and hull fouling of yachts, have been implicated in dispersal outside the species' native range.

Low-energy, intertidal, boulder/cobble beaches are generally considered the characteristic habitat, but in North America the crabs also utilize sand/pebble beaches, mussel beds, eelgrass beds and salt marshes, rock jetties, wooden bulkheads and pilings, and submerged and floating aquaculture gear (cages and spat collectors). In North America, populations move to subtidal depths during winter.

In its native range, Asian shore crab experiences water temperatures of approximately 0°C in winter in the north, and up to 28°C in summer in the south. Corresponding temperatures on the Atlantic coast of North America may be found between Atlantic Canada and Florida.

The maximum sizes in Japan are 42.4 mm and 39.0 mm in carapace width for males and females, respectively, corresponding to a maximum lifespan of around eight years (Fukui 1988). In New Jersey, a maximum size of 43.9 mm has been recorded for males (McDermott 1999).

In most areas inhabited in the USA, females are ovigerous between April and September and produce at least two broods per season. Large females could produce

broods of >40,000 embryos. Larval development occurs in 16 d at 25°C to 55 d at 15°C. At temperatures < 25°C, larval development occurred only at salinities above 20 ‰. Females become mature at approximately 12 mm CW after approximately one year.

Asian shore crab populations increased rapidly after establishment in the eastern USA, and in less than a decade outnumbered all other crab species combined in some sites. Competition for food and shelter has been reported with the green crab (*Carcinus maenas*), mud crabs (*Panopeus herbstii*, *Dyspanopeus sayi*, and *Eurypanopeus depressus*), and the wharf crab (*Armases cinereum*). Asian shore crab eats algae, eelgrass (*Zostera marina*), bivalves, gastropods, crustaceans, and polychaetes.

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